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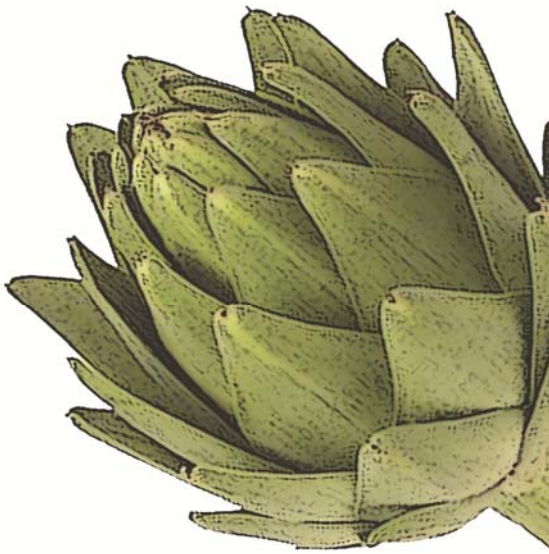

Verticillium Wilt: A Threat to Artichoke Production

The globe artichoke (*Cynara cardunculus* L. var. *scolymus* (L.) Fiori (=*C. scolymus* L.)) (diploid, 2*n* = 34) is the most important botanical variety of the species, which also includes *C. cardunculus* L. var. *altilis* DC. (=*C. cardunculus* L. var. *cardunculus*), the cultivated cardoon, and *C. cardunculus* L. var. *sylvestris* (Lamk) Fiori, which comprises wild relatives. The genus *Cynara*, native of the Mediterranean Basin, belongs to the botanical family Asteraceae (=Compositae) and includes seven species besides *C. cardunculus*. It is widely accepted that *C. cardunculus* var. *sylvestris* is the ancestor of the other two varieties (55,120). Artichoke is an allogamous species that is mainly propagated vegetatively via "stumps" (basal stem pieces with attached root sections) or "ovoli" (axillary buds separated from the stumps), although a few cultivars are seed-propagated (101).

More than 120,000 ha of globe artichokes are cultivated in more than 25 countries worldwide that yield approximately 1,300,000 t of buds. This hectarage represents 2.5% of the world area cultivated to vegetables (51). Italy is the leading artichoke-producing country with more than 35% of world production. Spain ranks second with 19% of world production despite a 20% hectarage reduction during the last 5 years. Similar reductions of the cultivated area and production of artichokes have occurred in France, the United States, and, less markedly, in Greece (Table 1). Conversely, the crop hectarage has expanded greatly in other countries: over a 30-fold increase in Peru, twofold increase in China and Turkey, about 60% increase in Chile and Egypt, and nearly 20% increase in Algeria, Argentina, and Morocco. Additionally, the yield per cultivated area in countries such as Algeria, China, Morocco, Peru, and Turkey has recently achieved a level comparable with that of other countries. This may be a consequence of significant improvements in artichoke cultivation technology in those countries, where artichoke plantations have been established more recently than elsewhere. An overview of world production of artichokes was published recently (80).

Verticillium wilt, caused by the soilborne fungus *Verticillium dahliae* Kleb., is one of the main constraints for artichoke production worldwide. This disease was first reported on artichoke in Italy in the late 1920s (42,95). Subsequently, new reports were published from France (27), again in Italy (25,32,36), Spain (112), Chile (52), Greece (114), California (17), and Tunisia (67). Currently, Verticillium wilt occurs in all artichoke-growing areas.

Verticillium wilt is becoming an increasing concern in artichoke production because the rapid spread of the disease to new growing areas has led to declining production. For example, in the 1980s, the disease was found affecting artichoke crops in several Italian regions such as Apulia, Campania, Lazio, Sardinia, Sicily, and Tuscany. In Apulia, which is the most important Italian area of artichoke production, problems with Verticillium wilt led to a reduction in the area cultivated to artichoke in the Bari Province, and also extended rapidly to new plantations that had been established in the provinces of Brindisi, Foggia, and Lecce (2,33). A similar decrease in artichoke cultivation due to Verticillium wilt was observed in Chile (52,53). In Spain, Armengol et al. (3) underlined the spread of Verticillium wilt in the Comunidad Valenciana region in eastern-central Spain, the main artichoke-growing area in the country. They reported over 80% disease prevalence in fields of stump- and seed-propagated artichokes sampled during 1999 to 2002, with an average wilt incidence of 53.8%.

Symptoms of Verticillium Wilt on Artichokes

Disease symptoms initially appear in patches or on individual plants depending on whether the source of primary inoculum is infested soil or infected planting material, respectively. Subsequently, the disease progressively develops over larger areas coalescing throughout an entire field (Fig. 1). Initial symptoms consist of delayed sprouting and severe stunting of infected plants. Leaf symptoms begin on basal leaves, but younger ones can be affected as well, especially under high disease pressure (Fig. 2). Symptoms are often expressed on only half of the leaf blade, but less frequently can extend over the entire leaf. Affected leaf blades first show intense yellowing, that later progresses to severe wilting and necrosis. The area of the leaf blade initially affected by wilting usually does not enlarge over time, resulting in a leaf with a characteristic curved shape. Younger symptomatic leaves show chlorosis. Rather than wilting, they usually roll up toward the adaxial side of the leaf blade. Commonly, defoliation does not occur in wilt-affected artichokes.

Under controlled conditions in growth chambers, seed-propagated artichoke plants root dip–inoculated with *V. dahliae* develop severe chlorosis, wilting, and necrosis of basal leaves which pro-

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gress upward to reach the newly formed ones (Fig. 3). No defoliation occurs and plants may die within 60 days after inoculation depending upon experimental conditions (68). A similar wilt development has been observed in resistance screening of a large germplasm collection of wild artichokes under greenhouse conditions (G. Bubici, M. Amenduni, and M. Cirulli, *unpublished data*).

As with other Verticillium wilt diseases, xylem browning can be seen on transverse sections of stems and main veins of leaves, which is useful for diagnostic purposes (Fig. 4). Production of buds is drastically reduced in quantity, and quality is severely compromised as infected buds are generally smaller and malformed (37). In eastern-central Spain, artichoke is a perennial crop that may be grown for several cropping seasons. However, because of yield reduction and plant death, the crop may become unprofitable as it is maintained in production for more cropping seasons. Severity of symptoms in Verticillium wilt–affected crops increases progressively in the first growing season, reaching a maximum during the second season, often forcing many growers to abandon the second growing season when disease incidence increases (15).

V. dahliae and the Pathogenesis of Verticillium Wilts

Verticillium wilt of artichoke is caused primarily by *V. dahliae*, although *V. albo-atrum* Reinke & Berth and *V. tricorpus* Isaac can also infect artichokes (96). *V. dahliae* is a worldwide-distributed, strictly asexually reproducing ascomycete that is characterized by the formation of dark microsclerotia (clusters of thick-walled, heavily melanized cells) variable in size (15 to 50 µm, occasionally up to 100 µm) and shape (elongated to irregularly spherical) (Fig. 5). The fungus produces hyaline conidia (2.5 to 8.0 × 1.4 to 3.2 µm) aggregated in moist droplets at the tip of flask-shaped, uninucleate phialides (16 to 35 × 1.0 to 2.5 µm) which are arranged in whorls (verticils) on unbranched conidiophores (Fig. 6) (106). *V. dahliae* can grow and infect at 30°C, but not at 33°C, with an optimum growth range at 24 to 27°C depending on the strain (9,43,66).

Although specific information about the cycle of pathogenesis in Verticillium wilt of artichoke is still lacking, it is likely that characteristics of Verticillium wilt diseases in general apply to this host. *V. dahliae*–induced diseases are characterized by a wide host range of the pathogen, the ability of the fungus to survive many years as dormant microsclerotia free in soil or within plant debris, and fungal growth confined within the xylem during the pathogenic phase (63,92). *V. dahliae* is able to infect more than 400 plant species, including annual, herbaceous crops and weeds, as well as fruit, landscape, and ornamental trees, and shrubs (92). *V. dahliae* microsclerotia can remain viable in soil for up to 14 years (121). Soil infested with microsclerotia (5,44) and infected planting material (49,102,117) are important sources of inoculum. In soil, dormant microsclerotia are stimulated to germinate (multiple times) in response to root exudates from host and some nonhost plants (77,88,105). The effective rhizosphere influence of roots on microsclerotial stimulation averages about 100 µm (64). In most plants, *V. dahliae* can successfully penetrate the root epidermis and reach the cortical tissues; however, most cortical infections fail to reach the vascular tissues and establish vascular infections (54). Several authors have reported on preferential colonization sites that lead to successful vascular infections. However, studies using histological staining techniques or confocal microscopy combined with use of pathogen strains labeled with a gene coding for green fluorescent

Table 1. Harvested area and production of artichokes in the world (51)

	Harvested area (ha), and average production of the 5-year periods (t)[a]						
Country	**1978–1982**	**1983–1987**	**1988–1992**	**1993–1997**	**1998–2002**	**2003–2007**	**Latest variation[b] (%)**
Italy	52,343	50,083	48,381	49,796	50,417	50,120	–0.2
	(542,500)	(481,060)	(502,840)	(499,094)	(482,813)	(458,816)	(–8.5)
Spain	24,268	25,504	28,840	20,274	18,987	19,406	–17.7
	(293,352)	(302,981)	(405,020)	(284,165)	(282,247)	(245,367)	(–21.7)
France	14,775	13,800	14,247	13,285	12,265	10,337	–24.4
	(100,484)	(62,920)	(89,278)	(69,911)	(70,993)	(53,716)	(–31.8)
China	–	–	3,000	4,200	7,200	9,600	100.0
	–	–	(8,000)	(14,000)	(31,800)	(55,400)	(208.9)
Argentina	3,158	3,627	3,580	3,880	4,420	4,640	24.3
	(61,500)	(70,626)	(71,400)	(74,400)	(83,200)	(88,400)	(22.4)
Peru	176	150	110	214	353	3,416	1,604.3
	(1,240)	(1,205)	(975)	(2,351)	(4,920)	(54,033)	(2,427.3)
Chile	2,348	2,528	2,182	2,526	3,173	4,100	60.7
	(17,550)	(20,585)	(16,710)	(18,306)	(24,445)	(31,600)	(61.9)
Egypt	1,794	1,932	2,665	2,349	3,193	3,893	63.1
	(32,152)	(40,200)	(62,375)	(37,119)	(59,657)	(75,771)	(63.6)
United States	4,047	4,914	4,259	3,682	3,604	3,134	–23.6
	(43,297)	(50,777)	(54,135)	(43,970)	(44,932)	(39,506)	(–16.7)
Morocco	5,600	1,840	1,635	2,148	2,792	3,290	17.4
	(31,800)	(21,720)	(21,796)	(27,310)	(36,586)	(52,887)	(90.0)
Turkey	1,078	1,260	953	1,453	2,320	2,680	89.7
	(7,360)	(10,000)	(10,248)	(17,120)	(26,060)	(32,694)	(130.9)
Algeria	2,606	1,342	1,128	1,708	3,928	2,692	25.6
	(13,716)	(6,560)	(6,481)	(13,636)	(36,899)	(36,861)	(138.5)
Greece	3,606	3,293	2,720	2,440	3,100	2,741	–9.6
	(40,162)	(31,744)	(31,111)	(26,800)	(33,205)	(30,806)	(–5.5)
Tunisia	2,220	1,470	1,592	2,244	2,630	2,186	7.6
	(14,920)	(12,300)	(12,300)	(19,400)	(18,500)	(14,400)	(–7.0)
Other countries	522	598	2,159	2,636	3,018	2,980	66.8
	(5,911)	(6,972)	(25,455)	(31,372)	(36,249)	(32,898)	(55.2)
World	118,541	112,340	117,452	112,835	121,400	125,214	7.5
	(1,205,945)	(1,119,649)	(1,318,123)	(1,178,954)	(1,272,505)	(1,303,156)	(6.9)

[a] Production data are reported in parentheses.

[b] Latest variation = $\left(\frac{\text{Average}_{2003-2007}}{\text{Average}_{1978-2002}} \times 100\right) - 100$. Latest variation of production data is reported in parentheses.

proteins, revealed that pathogen colonization of the root cap and the root elongation zone could lead to vascular invasion in several crops (20,54,116). Infection of the xylem vessels is required for disease development. Prior to symptom development, *V. dahliae* produces conidia within xylem vessels that are dispersed upward in the transpiration stream (Fig. 7), leading to a rapid and systemic colonization of the plant, including eventual infection of neighboring vascular and cortical tissues. The plant reacts to pathogen penetration and colonization by producing callose deposits in the paravascular parenchyma, and gels and tyloses in the vessels. Infected vessels become infused by preformed phenolic compounds, which are responsible for vascular browning after oxidation by polyphenol oxidases. Presence of fungal structures, gels, and tyloses in the xylem vessels contribute to vascular occlusion, which retards vascular flow in the stem and especially in leaf petioles. Vascular occlusion in leaf petioles results in plant wilting more than does occlusion in the stem (8). Fungal lytic enzymes, plant hormones, and phytotoxins are also implicated in the development of the Verticillium wilt syndrome (8). In some plants, the appearance of foliar symptoms is coincidental with the transition from vegetative to reproductive growth stages of the host (49,111). As the foliage begins to senesce and die, the fungus leaves the xylem elements and colonizes the surrounding nonvascular tissues of leaves and stems where microsclerotia are soon formed in senescent tissues (60,79). The amount of microsclerotia formed varies

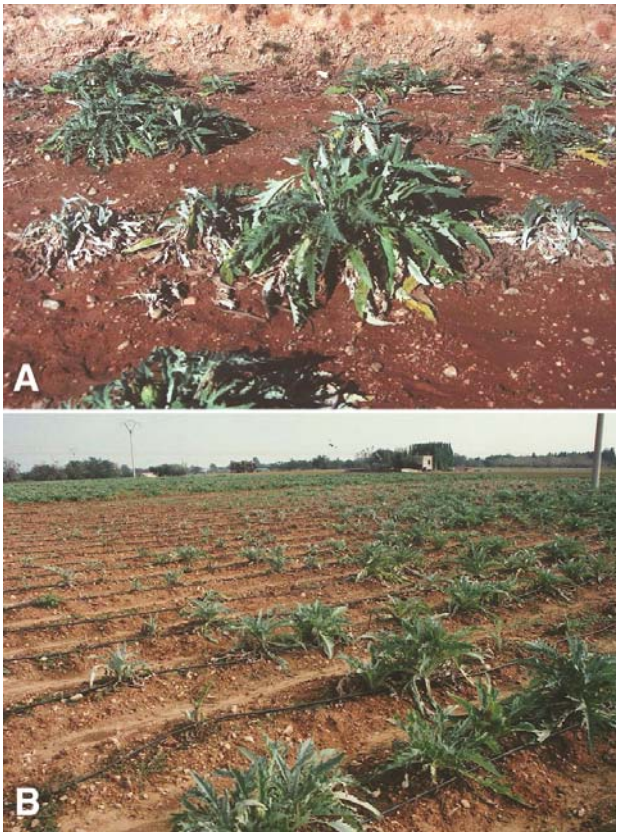

Fig. 1. Field symptoms of Verticillium wilt in stump-propagated artichokes: **A,** initial stage of disease attack, and **B,** severe disease extended over a large area.

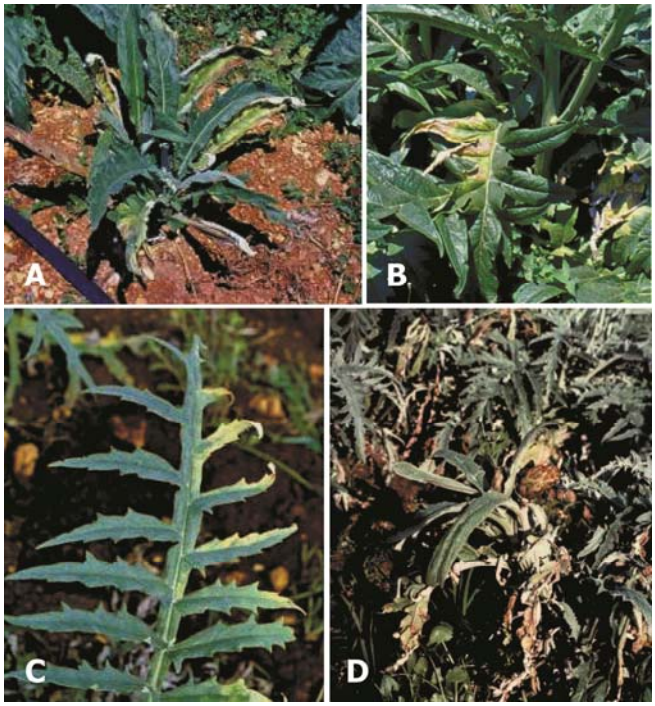

Fig. 2. Foliar symptoms of Verticillium wilt in stump-propagated artichokes: **A,** chlorosis and necrosis in basal leaves, **B and C,** intense yellowing on half of blade or leaflets of young leaves, and **D,** severe leaf wilting and necrosis.

Fig. 3. Disease reaction of seed-propagated, 6-week-old plants of artichoke hybrid cv. Nun 6374 root dip inoculated in a conidial suspension of artichoke isolates of *Verticillium dahliae* and incubated at 20 to 24°C in the greenhouse for 2 months. HSI = heterokaryon self-incompatible, VCG = vegetative compatibility group. Note that no defoliation occurred even in plants inoculated with isolates of VCG1A that comprise the cotton- and olive-defoliating pathotype of *V. dahliae* (68).

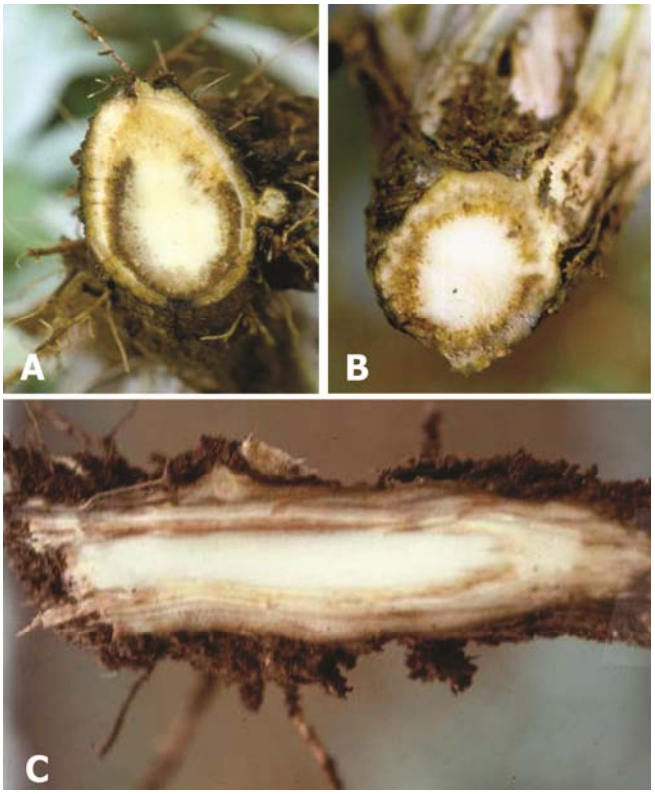

Fig. 4. Dark brown xylem discoloration in **A and B,** transverse, and **C,** longitudinal sections of roots **(A and C)** and stem **(B)** of Verticillium wilt–affected artichokes.

depending on the fungal isolate (74), host cultivar (89,118), and temperature (107). Microsclerotia are gradually released into the soil as infected host residues decompose. Conidia or mycelia in soil do not contribute to long-term survival of the pathogen (58).

Population Biology of *V. dahliae* from Artichokes

In general, natural populations of *V. dahliae* are conceived as host adapted rather than host specific, i.e., they display cross pathogenicity but are more virulent (herein defined as the relative capacity of a pathogen strain to cause disease, as indicated by the intensity of symptoms caused on individual hosts or host genotypes) to the host from which they were isolated (17,48,73,97,110). Thus, under selection pressure, some pathogen strains can adapt to new hosts so that isolates causing severe disease in one host can potentially derive from those infecting other hosts (73,97,111). In addition, more specific pathogenic adaptation may occur to some hosts or cultivars, giving rise to the establishment of pathotypes (90,103) and pathogenic races (1,47,117). Unraveling the existing host adaptation in *V. dahliae* populations may help in choosing alternative crops for crop rotation schedules. Limited information is available concerning the host-specificity of isolates of *V. dahliae* infecting artichoke. In France, one isolate from artichoke was found virulent on eggplant, melon, and pepper, but not on tomato (27). Studies in Italy showed first that two isolates from artichokes in Apulia (southeast of the country) were pathogenic on cantaloupe melon, carosello (a local vegetable from southern Italy, the cucumber melon, *Cucumis melo* var. *chate*), eggplant, and watermelon, but not on cucumber, pepper, and tomato (37). Further work indicated that 29 similar isolates were highly virulent on eggplant and carosello, moderately virulent on watermelon and melon, and confirmed not pathogenic on cucumber, pepper, and tomato (31). Similarly, pathogenicity assays on 11 vegetables often used in crop rotations showed 12 *V. dahliae* isolates from artichokes in eastern-central Spain to be highly virulent on artichoke, cardoon, eggplant, and watermelon, but nonpathogenic to cauliflower, cucumber, lettuce, pepper, and pumpkin (14).

Overall, the wide host range of *V. dahliae* isolates and the few known cases of pathogenic races in its populations have led to the perception that little genetic variation exists within the species (62). However, in addition to the few examples of specific adaptation, a continuum of virulence has been found to occur within populations of *V. dahliae* infecting some crops, such as cotton, potato, and tomato (4,59,70), suggesting that a considerable genetic variation must occur at loci other than those coding for specific virulence traits. In fact, studies during the last decade have demonstrated that genetic diversity within *V. dahliae* populations is higher than previously thought, and that limited understanding of the nature of such diversity has hampered the efficacy of Verticillium wilt management (6,72,99).

Understanding the population biology of *V. dahliae* is important for disease management through risk assessment, as well as development and deployment of resistant cultivars, exploring the pathogen potential for evolving new strains with improved pathogenicity traits, and preventing their introduction into new areas. The population biology of *V. dahliae* has been studied mainly by means of vegetative compatibility analysis (72,94,99) as well as analyses of the fungal DNA, including random amplified polymorphic DNA (RAPD), restriction fragment length polymorphism (RFPL), amplified fragment length polymorphism (AFLP), and specific primers (17,24,68,84,93,97). Vegetative compatibility is determined by the *het* (heterokaryon incompatibility) loci-controlled ability of individual fungal strains to undergo hyphal anastomosis and form heterokaryons. Fungal isolates that are vegetatively compatible are placed in the same vegetative compatibility group (VCG) (72,78). Because sexual recombination is unknown in *V. dahliae*, hyphal anastomosis followed by formation of a heterokaryon is a prerequisite to genetic exchange and eventual parasexual genetic recombination among different isolates (61,92). Therefore, *V. dahliae* iso-

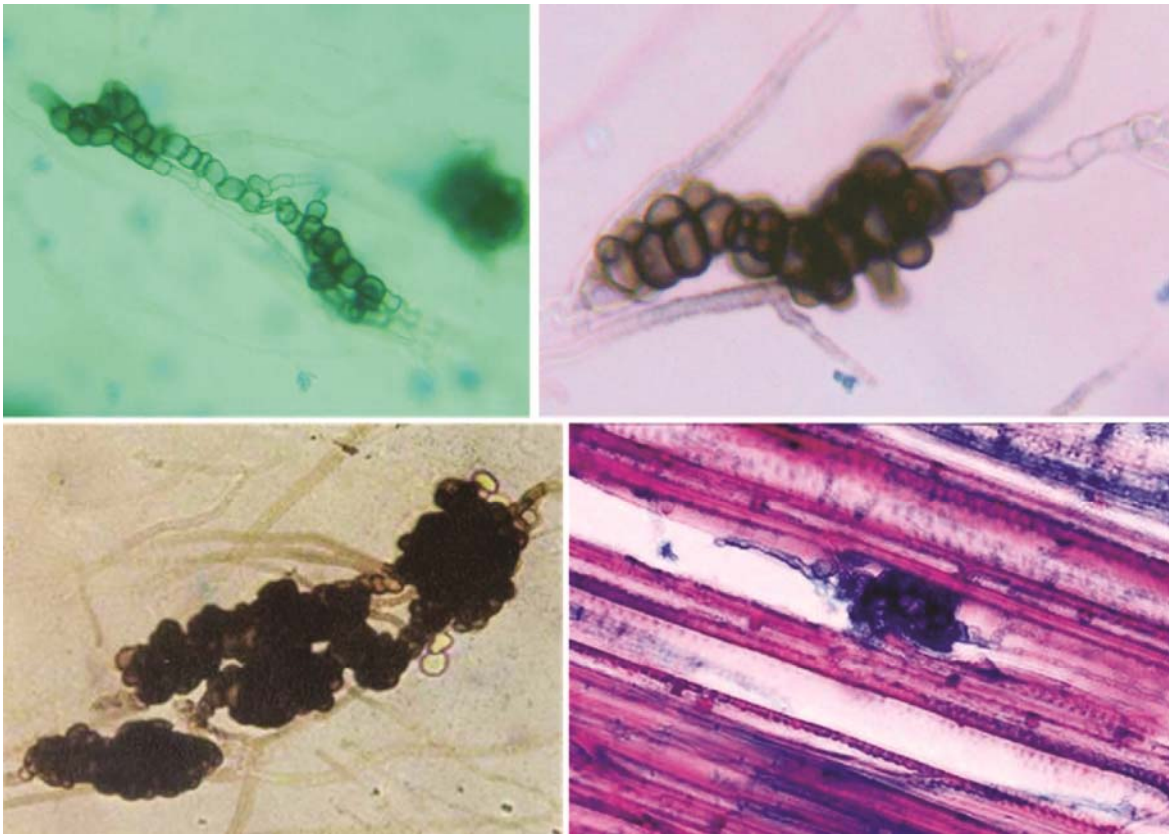

Fig. 5. Microsclerotia of *Verticillium dahliae* formed in water agar and within a xylem vessel of an infected plant. Note different stages of microsclerotial development and morphology. Elongated microsclerotia are characteristic of the cotton- and olive-defoliating *V. dahliae* pathotype.

lates in different VCGs are thought to be genetically isolated populations which may vary in a number of ecological, physiological, and virulence traits (72,99). Six VCGs (VCG1 through VGC6) have been identified using complementing nitrate-nonutilizing (*nit*) mutants of isolates from diverse hosts and geographic origin worldwide (10,16,28,69,72,109). VCG1, VCG2, and VCG4 were further divided into two subgroups (designated A and B) based on the frequency and vigor of complementation (10,70,108). Strausbaugh et al. (109) assigned a single isolate to a new VCG, VCG5; however, there are no references that other isolates have been included in this VCG since then. A set of isolates and *nit* mutant testers have been described that facilitate an internationally uniform system for VCG identification in *V. dahliae* (69,70,108,109). The generalized use of this set of testers would help to standardize VCG studies and thus the international exchange of information about VCG in *V. dahliae* (72,99). AFLP analysis of *V. dahliae* genomic DNA demonstrated that isolates within a VCG subgroup are genetically similar, to the extent that AFLP clustering of isolates correlates with VCG subgroups regardless of the host source and geographic origin (39).

V. dahliae populations infecting artichokes in three provinces of eastern-central Spain, the country's main artichoke-growing region, were typed to VCGs and found harboring limited VCG diversity. Out of 107 isolates examined, 96% were VCG2, with 67% being VCG2B and 29% VCG2A; one isolate was VCG1A; three were VCG4B; and two were heterokaryon self-incompatible (68). VCG2B was distributed across the region and was the most prevalent VCG in northern areas, whereas 84% of VCG2A isolates were recovered from southern areas. The isolate's VCG correlated with its virulence on artichoke. Collectively, isolates in VCG2B and VCG4B were more virulent to artichoke hybrid cvs. Nun 6374 and Nun 9444 than those in VCG2A (68). Interestingly, the sole isolate in VCG1A was the least virulent and did not induce the defoliating syndrome that characterizes the disease reaction of cotton and olive to isolates in this VCG (Fig. 3) (75,76,86,90). Conversely, this VCG1A isolate was highly virulent to cotton (68). VCG1A isolates from cotton and olive show cross-virulence on these hosts (98,104). Knowledge regarding prevalence and virulence of specific *V. dahliae* isolates on artichokes in the region is critical for disease management and indicates that control strategies, such as use of resistant cultivars and crop rotation, should target mainly VCG2B because of its high prevalence and virulence, as well as limited host range (14).

Results from that study also indicated that VCGs do not fully describe the overall genetic diversity among strains of *V. dahliae*. In fact, VCG2B isolates from artichoke in eastern-central Spain were genetically heterogeneous because they either complemented with the international reference VCG testers (and constituted subgroup VCG2Br) or failed to do so but complemented with VCG2Br isolates (and constituted subgroup VCG2Ba) (67). This genetic heterogeneity was further supported by diversity in the polymerase chain reaction (PCR) markers of 334 and 824 bp that previously were associated with the cotton and olive defoliating (D) or nondefoliating (ND) *V. dahliae* pathotypes, respectively (41,84,85). Thus, all 21 artichoke isolates of VCG2Ba and 43% of the 51 VCG2Br isolates in that study carried the 334-bp marker, but the remaining 57% of VCG2Br isolates had the 824-bp marker in common with isolates of VGC2A and VCG4B (68). Moreover, phenetic analysis of AFLP fingerprints of *V. dahliae* isolates from artichoke, cotton, and olive of diverse geographic origin grouped VCG2B artichoke isolates into two distinct clusters that correlated with the amplification of PCR markers of 334 bp ($VCG2B^{334}$) or 824 bp ($VCG2B^{824}$); $VCG2B^{334}$ isolates grouped with cotton and olive isolates of VCG1A (39). A further phylogenetic analysis of AFLP data identified two main lineages (I and II) that comprised different VCGs. Artichoke isolates of $VCG2B^{334}$ were placed together with isolates of VCG1A in lineage I, whereas $VCG2B^{824}$ isolates were in lineage II, suggesting that VCG2B is of polyphyletic origin (40). Polyphyly (i.e., evolving independently more than once) in VCG2B may be important for the management of Verticillium wilt

Fig. 6. *Verticillium dahliae* conidiophore. Note phialides arranged in whorls and conidia at the tip of phialides.

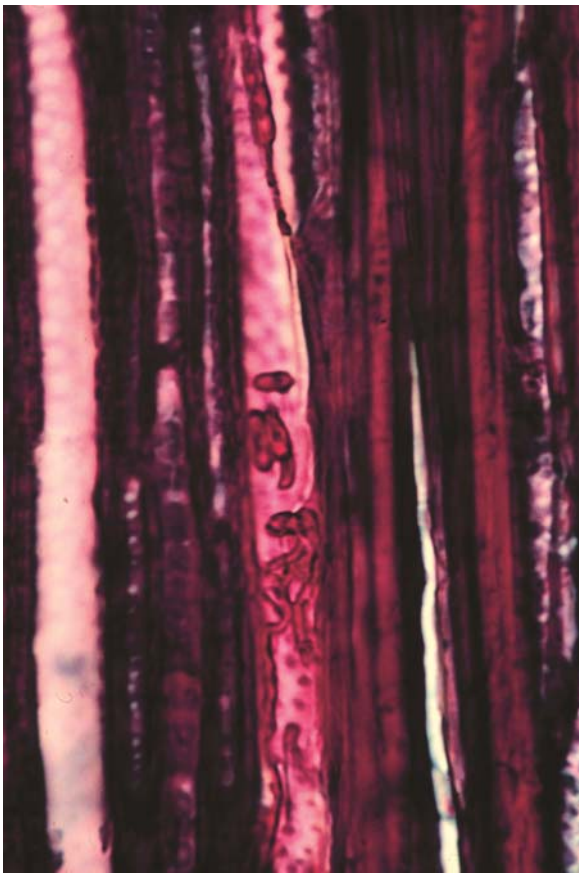

Fig. 7. Conidia of *Verticillium dahliae* in a xylem vessel of an infected plant.

of artichokes because it implies that the ecological, physiological, and/or virulence traits of isolates may vary across locations. Appearance of VCG2B^{334} isolates might result from a regressive change to recover ability of complementing with isolates of an ancestral, compatible VCG, as an alternative of acquiring a common set of *het* loci with them by means of independent mutation events (40). In that scenario, VCG2B^{334} isolates probably derived from VCG1A isolates (or from a recent common ancestor) because, as a group, VCG2B^{334} is molecularly more similar to VCG1A than to VCG2B^{824}. VCG1A must have existed earlier in the artichoke-growing region at eastern-central Spain, as suggested by the identification of cotton crops in this region infected by defoliating VCG1A isolates (68).

Recently, molecular markers based on microsatellites and polymorphic sequences were used to assess the genetic structure of a *V. dahliae* population from eastern-central Spain. The population comprised 30 isolates obtained from artichoke and 20 isolates from potato grown in the same production areas where both crops are used in rotations. The relatively high genetic differentiation observed among subpopulations from both hosts and the high genotypic diversity suggest a degree of differentiation between populations of the pathogen from different hosts, which could have resulted from the adaptation of *V. dahliae* from the original, resident population to different hosts (13).

Disease Cycle and Epidemiology

V. dahliae microsclerotia in infested soil or mycelia in the vascular rings of symptomless planting material (off-shoots or stumps) are the only inocula giving rise to disease in artichokes (30). Verticillium wilt is a monocyclic disease, i.e., it has only one cycle of pathogenesis per cropping season and the resulting inoculum does not give rise to new infection and disease within the same season.

The epidemiology of Verticillium wilt diseases is driven mainly by inoculum density in soil. However, the combined effects of several other factors are involved, including plant/water relationships, soil nutrients, soil and air temperature, and plant and root densities (45). In addition, the ability of *V. dahliae* to infect many weed species may play an important role in the epidemiology of Verticillium wilts. Regardless of whether infected weeds show wilt symptoms, they may serve as alternative hosts contributing to maintenance or even increase of *V. dahliae* inoculum in soil (87,113,117). Verticillium wilt varies seasonally relative to fluctuations of air temperature and succeeding plant growth stages. Disease incidence and severity are usually higher in spring. Successful isolation of the pathogen from affected tissues also varies seasonally. Armengol et al. (3) found that the frequency of *V. dahliae* isolation from diseased artichokes was higher in autumn, decreased or null in winter, and increased again in spring. Whether differential isolation reflects seasonal differences in the presence of the pathogen or some barrier when the pathogen is present was not determined. Seasonality in the frequency of *V. dahliae* isolation from affected tissues is common in olive and other woody hosts (22,63).

The likelihood of plant infection by *V. dahliae*, and thus of Verticillium wilt incidence and severity, is directly related to the population density of microsclerotia in soil. Inoculum density increases as debris of infected hosts decay over seasons, thus releasing embedded inoculum. For example, monoculture of cotton cv. Acala SJ-2 in California increased the inoculum density of *V. dahliae* by 13 to 15 microsclerotia (ms) per gram of soil per year (65). This amount may increase several-fold in the case of hosts such as lettuce (111). Thus, the range of crops used in rotation with artichokes is an important factor in the epidemiology of Verticillium wilt. In eastern-central Spain, common rotation schemes for artichoke production include repeated potato crops. Disease surveys of potato crops grown in rotations with artichokes in Alicante Province in that region revealed the occurrence of severe early dying disease and infections by *V. dahliae* (91). Further pathogenicity assays of a sample of 12 *V. dahliae* isolates obtained from potato in different locations demonstrated that they were all pathogenic to artichoke, although with a variable degree of virulence. A similar situation may occur in faba beans, often grown in rotation or intercropped with artichoke, which recently were found infected with *V. dahliae* in Castellón Province of eastern-central Spain (11). *V. dahliae* isolates from faba bean were of VCG2B, which was shown to be the most prevalent VCG on artichoke in that province and the most virulent to artichoke (11,68).

Studies by Armengol et al. (3) in eastern-central Spain demonstrated that an initial inoculum density as low as 1.5 ms g^{-1} of soil (assessed by the dry sieving technique and Anderson sampler using modified NP-10 medium [23,71]) resulted in a final disease incidence of 16 and 31.8% in the first and second year, respectively, after planting stump-propagated artichoke cv. Blanca de Tudela. Comparatively, planting the same field with seed-propagated artichoke plants of cv. Imperial Star resulted in no disease the first year and a 5% final incidence of Verticillium wilt in the second year. However, when the two types of planting material were used in a second field with an inoculum density of 15 ms g^{-1} of soil, more than 60% of plants were affected by the disease by 2 months after planting, and nearly 100% of them were infected by *V. dahliae* by the end of the cropping season. Armengol et al. (3) also found that the bud yield decreased significantly as disease incidence increased. Similarly, studies in California found that 85 to 98% incidence of Verticillium wilt caused 50% yield reduction of the seed-propagated cv. Imperial Star (18). The relationship between *V. dahliae* inoculum density in soil and the development of Verticillium wilt in artichoke was subsequently studied in more detail in 10 commercial fields located in eastern-central Spain (15). In those fields, the initial inoculum density of *V. dahliae* varied between 2.2 and 34.2 ms g^{-1} of soil at planting with stumps of cv. Blanca de Tudela. Berbegal et al. (15) found low but significant correlations (R^2 values ranging from 0.33 to 0.66) between soil inoculum density and disease incidence, symptom severity, or recovery of the pathogen from the plant, which were best described by negative exponential models. According to the authors, this low correlation under field conditions may reflect the effects of factors influencing host–pathogen relationships, including cultural practices, environmental conditions, and variation in virulence among *V. dahliae* isolates prevailing in the soil. Inoculum densities ranging from 5 to 9 ms g^{-1} of soil were associated with a mean disease incidence of about 50%. These authors studied the dynamics of microsclerotial populations in soil and disease progression in three of the 10 fields during two consecutive growing seasons. While the inoculum density decreased significantly by the end of the first growing season and then increased slightly at the end of the second season, the severity of symptoms and incidence of infected plants were the highest during the second growing season. The decrease in inoculum density might be explained by microsclerotia germination near the plant roots and/or microbial degradation. These phenomena would lead to a decline of microsclerotia population in soil until new propagules are released into the soil from infected tissues by the end of the season.

Disease Diagnosis

Accurate diagnosis is the first step for successful management of Verticillium wilt in artichokes. Because visible symptoms may be insufficiently diagnostic, demonstrating the presence of *V. dahliae* in affected tissues by direct isolation of the pathogen is often advisable to confirm the diagnosis. *V. dahliae* can be easily isolated from the leaf main vein or main stem vascular tissues in affected artichoke plants by conventional isolation procedures on water agar amended with Aureomycin (1 liter of distilled water, 20 g of agar, 30 mg of Aureomycin), but the efficacy of this method is influenced by the time of sampling during the cropping season. In pure culture, *V. dahliae* can be identified by its white mycelium, verticillate conidiophores, and microsclerotia.

Isolations from underground plant parts can yield *V. tricorpus* in addition to *V. dahliae* (96). *V. tricorpus* is a weak pathogen that causes mild foliar symptoms and no significant reduction of plant growth in artificially inoculated artichokes (96). *V. tricorpus* forms

verticillate conidiophores, microsclerotia, resting mycelium, and chlamydospores. *V. tricorpus* develops large and irregularly shaped microsclerotia on potato dextrose agar, which can be morphologically differentiated from those formed by *V. dahliae* (i.e., smaller and oval to elongated microsclerotia) and often produces a diffusible yellow pigment that helps in differentiating it from *V. dahliae* (66,106). Also, on ethanol agar, *V. dahliae* forms large microsclerotia and abundant dark hyphae, whereas *V. tricorpus* does not form microsclerotia, but always forms dark mycelium (57).

Diagnosis of Verticillium wilt in artichokes can also be achieved through detection of *V. dahliae* in symptomatic or asymptomatic plant tissues by using molecular detection procedures developed for other hosts. Recently, Collado-Romero et al. (38) developed a multiplex-nested PCR procedure and specific primers that allow detection of *V. dahliae* in symptomless but infected artichokes, as well as the identification of the VCG of isolates, i.e., VCG1A or VCG2B^{334}, VCG2A/VCG4B, and VCG2B^{824}. This novel multiplex-nested PCR assay proved more efficient in detecting the pathogen than conventional isolation, allowed *V. dahliae* detection and VCG identification in symptomless but infected plants that had yielded false negatives by conventional isolation, and helped to demonstrate that several *V. dahliae* VCGs may infect a single artichoke plant. This detection technique may be of use for certification of artichoke planting material free from the pathogen, as well as for predicting the severity of Verticillium wilt epidemics in artichokes.

Management Strategies

Since Verticillium wilt is a monocyclic disease, its management is best achieved by excluding the pathogen, as well as by reducing primary inoculum levels and/or efficiency. Therefore, key disease control measures for the management of Verticillium wilt in artichokes are: (i) use of pathogen-free planting material; (ii) site selection to avoid planting into high-risk soils; (iii) reduction or elimination of *V. dahliae* inoculum in soil; (iv) protection of healthy planting material from infection by residual inoculum in soil; and (v) use of resistant cultivars (2,30,34,35,37,114). Overall efficacy of these measures increases if they are combined in an integrated disease management (IDM) strategy as recommended against other Verticillium wilt diseases (21,50,100). Furthermore, management of plant diseases by means of IDM strategies and minimum use of chemicals will be enforced in the European Union (EU) member countries by the year 2014 as a result of the Strategy on the Sustainable Use of Pesticides adopted by the European Commission (EC) (http://europa.eu/legislation_summaries/internal_market/single_market_for_goods/chemical_products/l28178_en.htm).

Use of *V. dahliae*–free planting material. *V. dahliae* can be spread in planting material originating from apparently healthy plants (30). Therefore, the common practice of selecting artichoke planting material based solely on the absence of disease symptoms should be disregarded (3). Thermotherapy by hot water treatment is of use to eliminate or reduce *V. dahliae* in latent artichoke stumps. Márquez et al. (81) showed that these stumps tolerate a hot water treatment at 49°C for 20 to 30 min with neither decrease in sprouting after planting nor reduction of the normal growth and bud yield compared with untreated controls. In a subsequent study, latent artichoke stumps infected by *V. dahliae* were treated at 46°C for 45 or 60 min, 47°C for 45 or 60 min, 48°C for 30 or 45 min, and 49°C for 30 or 45 min. Recovery of *V. dahliae* by isolating from internal tissues after treatment was significantly reduced compared with 16% recovery of the pathogen in untreated stumps. Hot water–treated and –untreated stumps were planted in *V. dahliae*–free soil and development of Verticillium wilt was monitored during the next two cropping seasons. *V. dahliae* was isolated from 16% of the untreated plants in the first cropping season. Conversely, the pathogen could not be isolated from plants receiving any of the other treatments, except heating at 46°C for 45 min, for which *V. dahliae* infection was reduced by 58%. In the second cropping season, *V. dahliae* infection in the untreated plants reached 31.5%, but none of the plants heated at 46°C for 60 min, 47°C for 45 or 60 min, or 49°C for 30 or 45 min yielded the pathogen. Conversely, *V. dahliae* was isolated from plants treated with hot water at 46°C for 45 min, 48°C for 30 min, or 48°C for 45 min, but infection was reduced by 82, 94, and 73%, respectively. Therefore, dipping latent artichoke stumps in water at 49°C for 30 to 45 min would be effective for eradicating *V. dahliae* from symptomless stumps and could be useful to establish fields of pathogen-free mother plants for supplying certified planting material to artichoke producers (31).

Site selection for the establishment of new plantings. Proper selection of the planting site optimizes the use of *V. dahliae*–free planting material in noninfested soils. For that purpose, it is critical to have accurate information on the disease history of the field with regard to production of susceptible crops for which cross virulence of *V. dahliae* isolates is known (see Population Biology section above). Also, disease risk assessment based on the relationship between inoculum density and disease incidence can be done by estimating the inoculum density in soil at planting sites, thus avoiding those with high risk for severe disease (see sections above: Disease Cycle and Epidemiology, and Disease Diagnosis). In particular, information on VCG of *V. dahliae* isolates prevailing in potential planting sites would allow avoiding use of soils infested with highly virulent isolates of VCG2B. Existing methods used to quantify *V. dahliae* microsclerotia in soil have been reviewed by Goud and Termorshuizen (56). Methods often used in risk analysis studies are based on dry and wet plating on semiselective media. Dry and wet plating methods do not differ in detection limits, but the former are less variable at higher inoculum densities and more variable at lower ones. These authors concluded that most quantification methods are soil-type dependent, but also useful for disease prediction within certain soil (56).

Soil disinfestation. Soil fumigation and soil solarization, either individually or in combination, have been successfully used for the control of Verticillium wilt in artichokes. Soil fumigation with methyl bromide and dazomet significantly reduced inoculum density of *V. dahliae* in soil (30). A comparative study on the efficacy of several fumigation treatments for control of the disease was done by Cebolla et al. (26) in artichoke fields in eastern-central Spain during two consecutive growing seasons. Treatments with 1,3-dichloropropene (Telone II emulsifiable) at 18 g m^{-2} followed by metham sodium at 72 g m^{-2}, the mixture of 55.4% 1,3-dichloropropene and 32.7% chloropicrin (Agrocelhone emulsifiable) at 40 g m^{-2}, all applied with irrigation water, and methyl bromide at 30 g m^{-2} under Virtually Impermeable Film, effectively controlled Verticillium wilt and increased bud yield in the first growing season compared with the control. In the second growing season, there was an increase in disease incidence and plant mortality in all treatments that resulted in an overall yield reduction of 46% compared with that achieved in the previous growing season. Soil disinfestation with metham sodium in irrigation water, usually without tarping of soil with a plastic sheet, has now become the most frequent treatment of soils for artichoke production in eastern-central Spain because of the relatively low cost and easy application (26). Nevertheless, several constraints may limit the future use of metham sodium for soil disinfestation. In moist soil, metham sodium undergoes decomposition to methyl isothiocyanate, the active compound that possesses broad-spectrum biological activity in soil (82,115). However, methyl isothiocyanate is prone to enhanced biodegradation in soil by adaptation of microbial populations to use the compound as an energy source. This adaptation may be induced by repeated or even single applications of metham sodium to a field, thus seriously compromising its efficacy (46,82,119). Furthermore, the use of those fumigants that have been tested against Verticillium wilt of artichoke will not be allowed in the EU in the future. A revision of nearly 1,000 active ingredients marketed since 1993 has been recently completed by the EC within the framework of EEC Directive 91/414. Of those, only 71 fungicides and 16 biocontrol agents, but no fumigants, have satisfied the established harmonizing criteria and are now approved for use in the EU.

For the above reasons, there is a need to develop new management strategies for the control of Verticillium wilt of artichokes that meet the established requirements. In a 2-year study in eastern-central Spain, Berbegal et al. (12) compared the efficacy of fresh cauliflower residue amendments alone or with a low dose of metham sodium, combined with or without soil solarization, for the control of Verticillium wilt of artichoke in two commercial fields. Soil solarization reduced inoculum of *V. dahliae* and the incidence of Verticillium wilt, but no added benefit was obtained when solarization was used with cauliflower residue amendments. Treatments with cauliflower residue amendments and low doses of metham sodium maintained low inoculum densities in soil of experimental fields until the end of the growing season and significantly reduced disease incidence. Also, studies in Greece showed satisfactory control of Verticillium wilt of artichoke by soil solarization (114). Both soil solarization and its combination with a reduced dose (34 g m^{-2}) of methyl bromide were effective in the control of the disease during three successive growing seasons. These two treatments significantly reduced the population of *V. dahliae* microsclerotia in soil, and this reduction was positively correlated with significant reductions in disease incidence as well as with increased bud yield. In addition, Tjamos and Paplomatas (114) found that natural populations of the soil-inhabiting fungus *Talaromyces flavus* increased and survived better in solarized soil than in soil solarized and fumigated. Because this fungus has been shown effective in biocontrol of Verticillium wilts, these authors reasoned that such increases in the *T. flavus* population might be partially involved in the control effects of solarization on the pathogen and the disease. Similarly, experiments in Italy showed that soil solarization reduced the severity of Verticillium wilt in newly established artichoke plantings, but the degree of control was insufficient to be commercially viable for artichoke growers (36).

The efficacy of combining soil disinfestation with use of pathogen-free planting material in the management of Verticillium wilt of artichokes would be enhanced if that material is further protected from infection by residual inoculum of *V. dahliae* in soil by using biocontrol agents. The efficacy of *T. flavus* for that purpose was assessed by Ciccarese et al. (29) and Cirulli et al. (36) in artichoke crops in southern Italy, who found no effect in the control of Verticillium wilt. More recently, work by Qin et al. (96) in California has shown that root treatment with low-virulent *V. tricorpus* strains reduced Verticillium wilt severity in artificially inoculated artichokes, and that this effect was improved if *V. tricorpus* was introduced into soil as a drench early enough in the production cycle.

Use of resistant cultivars. As for most Verticillium wilt diseases, use of resistant cultivars, when available, is the best control strategy for Verticillium wilt in artichokes. The high level of heterozygosis in artichokes as an allogamous species, together with the source of genetic variability occurring in the other two botanical varieties of *C. cardunculus*, which are genetically compatible with artichokes (120), are important bases for breeding programs aimed at producing new cultivars possessing desired traits. Germplasm collections of artichokes and wild relatives are available at the 'Istituto del germoplasma' of CNR (Consiglio Nazionale delle Ricerche, Bari, Italy), the 'Centro di studio sulle colture erbacee strategiche per l'ambiente mediterraneo' of CNR (Catania, Italy), and the 'Stazione sperimentale dell'Inra di Montfavet' (Avignone, France) (83). Determining the number of artichoke cultivars used in the world is difficult because of the extensive use of synonyms. For example, Bianco (19) cited over 286 cultivars, of which only a few are of economic importance (i.e., 'Blanca de Tudela', 'Violetto di Provenza', 'Violetto di Sicilia', or 'Catanese') (7). Unfortunately, no artichoke cultivar of commercial interest is resistant to Verticillium wilt at the present time.

The steps involved in breeding of artichokes (7,83) include:

1. selection cycles of vegetatively propagated clones identified within cultivars or ecotypes;
2. selection cycles of progenies obtained from artificial self-pollinations or crosses;
3. selection of inbred lines to be used for production of seed-propagated F_1 hybrids.

The only reports on breeding artichokes for resistance to Verticillium wilt come from the University of Bari, Italy. An early field screening of 130 artichoke accessions and cultivars, including genotypes possessing the "spiny" trait, was done using artificial inoculation. Among the screened germplasm, 10% were considered to be resistant/tolerant, and three lines were particularly worthy because of the absence of external symptoms and the low incidence of vascular browning. Since external symptoms and vascular browning were usually not correlated, especially in resistant plants, researchers carrying out the screening underlined the importance of using both indexes for screening and selecting germplasm. Later, the most interesting 11 clones were tested in a large-scale, 3-year field trial to confirm their wilt resistance reaction. Data from that test, and particularly from the third year of testing, allowed identification of six resistant clones (namely, clones 76, 8, 75, 104, 113, and 161) and five moderately resistant ones. Among the six resistant clones, clone 76 showed very few external symptoms and low vascular browning, and clones 8, 75, 104, 113, and 161 had very few external symptoms, but moderate vascular browning (35). Those clones were included in a breeding program to develop lines possessing a uniform and high Verticillium wilt resistance phenotype and valuable agronomic characteristics. Initially, on the basis of a mono/oligo-factorial genetic hypothesis, the breeding program consisted of three cycles of self-pollination and selection to increase homozygosis of resistance gene(s) (34). This program, which is still in progress, has included a number self-pollination cycles to eliminate undesired phenotypes separated from an open-pollination cycle to restore heterosis (M. Cirulli, *unpublished data*). Recently, a greenhouse screening of seed-developed wild and cultivated artichokes produced new resistant/tolerant lines that will be included as additional resistant parental lines in the breeding program (M. Cirulli, *unpublished data*).

Future Prospects for Effective Disease Management

Verticillium wilt is spreading in artichoke-growing areas worldwide, and it is becoming a threat to artichoke production and industry. This threat is likely to increase if artichokes are grown in monoculture or in rotation with susceptible crops, because of the ability of *V. dahliae* strains to adapt with increased virulence to new hosts under selection pressure. Effective management of the disease is best achieved by means of IDM strategies. However, susceptibility of currently available commercial cultivars, as well as regulations on availability and use of soil fumigants as a result of environmental concerns, are important constraints for the efficient management of this disease.

Development of commercial cultivars with either complete or partial resistance to Verticillium wilt is of utmost importance for management of the disease. Cultivars with partially resistant phenotypes would enhance the efficacy of other disease control measures incorporated into an IDM strategy. It is essential that isolates of the pathogen used for resistance screening are representative of lineages most prevalent and adapted to artichoke. When resistant cultivars are developed and utilized, strategies should be adopted to increase durability of the resistance genes that are deployed.

The use of stump-propagated planting material should be reinforced by the establishment of fields of *V. dahliae*–free mother plants and the implementation of certification schemes. The availability of a PCR-based protocol for *in planta* detection of pathogen strains would be of use for both aims. However, improvements are needed to increase the specificity of diagnosis and the utility of diagnostic practices on a commercial scale. An alternative approach to reduce the risk of introducing the pathogen in noninfested soil would be the use of seed-propagated planting material. However, more studies are warranted to comparatively assess development of the disease and yield between crops from each of those planting materials in soils with varying inoculum densities. Similarly, the effects of annual cropping of artichoke established

with either planting material on disease development and yield, as compared with perennial cropping, merit further study.

The effects of partially resistant cultivars and use of *V. dahliae*–free planting material would be optimized by proper selection of planting site through preplant assessment of *V. dahliae* population density in soil. Methods presently available for quantifying *V. dahliae* in soil, based on plating soil on semiselective media, are not sensitive or reliable enough to assure efficient implementation of that approach. These limitations can be overcome if new methods based on DNA technologies are developed that would allow sensitive and reliable quantification of specific strains of the pathogen in soil. Development of these methods should be a priority in studies aimed at management of Verticillium wilt of artichoke.

Soil solarization is useful for suppressing soilborne inoculum of *V. dahliae* and management of Verticillium wilt in artichokes in the absence of effective soil fumigants. However, effects of this technique on disease suppression can be further enhanced if combined with organic soil amendments and treatment of planting stock roots with biocontrol agents. Organic soil amendments and formulations of biocontrol agents are becoming commercially available. However, better understanding is needed of the mechanisms by which organic amendments interact with soil microbial communities and how that contributes to increased disease suppression, as well as on factors that determine sustained efficiency of biocontrol treatments in the control of the disease.

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